

EVIDENCE OF DIFFERENT ADAPTATIONS OF FLOWER COLOR VARIANTS OF ENCELIA FARINOSA (COMPOSITAE)

By DONALD W. KYHOS

It has long been recognized that plants are extremely sensitive to their environments, particularly to moisture and edaphic factors. In natural undisturbed environments one of the most notable ways this remarkable sensitivity is revealed is by the general lack of hybrids between sympatric species which in disturbed habitats do produce hybrids and their various derivatives. A most lucid account of this well known phenomenon is provided by Anderson (1949). In most instances such sympatric species differ by several to many externally visible features and many differ also by a number of less obvious aspects, including physiological attributes.

In such cases where a relatively large number of genetically determined attributes differentiate ecologically distinct taxa, it seems likely that their differing ecologic adaptations will be correspondingly complex and hence difficult to analyze. On the other hand, with taxa that differ by one or at most a few genetically controlled features, the probability is much greater that their ecologic adaptations are simple and relatively easy to analyze.

Moreover, in the case of taxa that differ in many genetically based traits there appears to be little chance of obtaining evidence of the manner in which they differentiated. For example, whether geographic isolation was necessary for their divergence and their sympatry secondary, or whether it is possible that in some instances ecological differentiation initially resulted from a very few, or even a single heritable difference which permitted the occupation of new, closely adjacent sites well within effective pollination range of the original population.

Thus it is apparent that there are at least two substantial advantages in seeking populations to study that are ecologically distinct, but which have few genetic differences. First, it is more likely that their ecologic adaptation can be discerned and successfully analyzed and second, they are rather more likely to provide evidence of their mode of origin.

If a relatively simple heritable difference can bring about an altered ecologic adaptation in natural environments, then it should be possible to find populations at this initial stage of ecologic divergence when they differ by one, or at most, a very few heritable attributes, as appears to be the case in *Ricinus* in Peru (Harland, 1946) and *Spergula* in Europe (New, 1958; 1959) and perhaps in Australian Eucalyptus (Barber and Jackson, 1957).

Encelia farinosa Gray also appears to provide an excellent opportunity to study populations at such an early, but very significant stage of

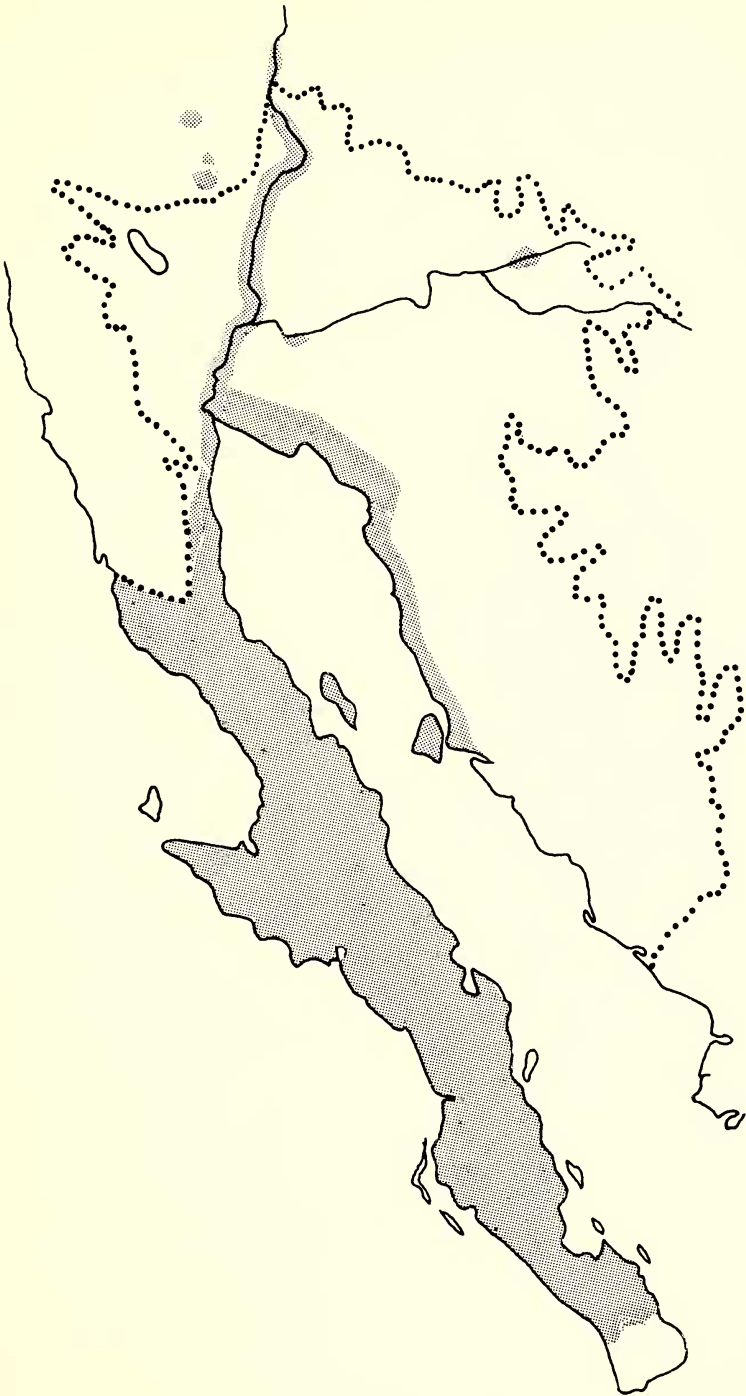
divergence. Many populations of *Encelia farinosa* in the Sonoran Desert are polymorphic for a single conspicuous feature. In California, southern Nevada, Arizona, and adjacent Mexico, *Encelia farinosa* occurs as variety *farinosa*, in which the ray and disk florets are a bright yellow and it also occurs as *E. farinosa* var. *phenicodonta*, which differs only in that the disk florets are a rich brownish-purple. Populations may consist entirely of one or the other of these varieties, or may contain both intermixed. This seemingly trivial phenetic difference would not ordinarily lead one to suspect that it is an expression of a more fundamental biological difference. However, an examination of what proves to be a rather remarkable distribution pattern of these two varieties of *E. farinosa* strongly suggests that this apparently simple flower color difference has a high selective value itself, is part of a pleiotropic expression of genetic material which is adaptive in some other less obvious feature, or that this flower color character is genetically very closely linked with some other factor of high selective value that is not readily discernible.

Distribution pattern.

Encelia farinosa is one of the dominant species of the Sonoran Desert, to which it is largely confined. It occurs in abundance from near the Cape region of Baja California, northward into the deserts of California, southern Nevada, southern Utah, Arizona, and Sonora, Mexico to Sinaloa (fig. 1). In the Cape region of Baja California, the southern-most populations of *E. farinosa* belong to var. *radians*, which occurs mainly in the tropical zone (Shreve and Wiggins, 1964). In the immediately adjacent deserts, *radians* is replaced by the very similar var. *phenicodonta*, which extends northward through the major portion of the Baja California peninsula to about San Felipe, Mexico. It is in this general region that the yellow disk flowered variety of *E. farinosa farinosa* appears and begins to replace *phenicodonta* in a most unusual pattern. In this more northern area of the Sonoran Desert, populations consisting entirely or predominantly of var. *phenicodonta* are largely confined to major river valleys. The yellow flowered populations of *E. farinosa* occupy much of the remainder of the northern Sonoran Desert, and are marginally sympatric with the brown disk flowered populations.

The writer first noticed this most unusual distribution pattern when making an approximately west to east transect across the Colorado River, near Blythe, California. While travelling south-eastward along the road from Rice, California toward Blythe, only yellow flowered *E.*

FIG. 1. *Distribution of Encelia farinosa.* The dotted line outlines the limits of the Sonoran Desert in northwest Mexico and the adjacent United States as defined by Shreve and Wiggins (1964). The shading denotes areas where *Encelia farinosa phenicodonta* occurs either in high concentrations or to the exclusion of *E. farinosa farinosa*. Five small disjunct *phenicodonta* localities are shown at about twice their proportionate size for clarity. *Encelia farinosa farinosa* occupies much of the remaining Sonoran Desert that is unshaded, as well as the area to the immediate north, included in this map.



farinosa populations were initially encountered until a point approximately 26 miles from Blythe was reached (16 miles due west of the Colorado River). The next mile of *E. farinosa* populations included *phenicodonta* individuals at a frequency of 5 percent. In the next 6-mile interval approaching Blythe the frequency of *phenicodonta* individuals in the populations progressively increased to 38 percent, and upon approaching to within 9.3 miles of Blythe the frequency of *phenicodonta* plants in the population gradually increased to 70 percent. Within Blythe and its environs, intensive agricultural practices have essentially eliminated *E. farinosa*, however, upon crossing the Colorado River into Arizona, *E. farinosa* is once again abundant. Proceeding east from the Colorado River along U.S. Highway 60-70 for the first two miles only *phenicodonta* individuals are encountered and with each mile eastward the frequency of this taxon continually declines, until at 13 to 14 miles east of the Colorado River, *E. farinosa* populations consist of less than 7 percent *phenicodonta* plants. Still farther eastward only yellow flowered populations are encountered.

The well defined cline revealed by this initial transect suggested that *phenicodonta* individuals would probably be concentrated in other areas of the Colorado River valley to the north and south of Blythe, California. Much of the Colorado River valley to the south of Blythe is under intensive cultivation, and still farther south the few areas near the Colorado River that are readily accessible lack *E. farinosa*. This is also the case on both the Arizona and California sides of the Colorado River at Yuma. Somewhat to the north of Yuma, as the Picacho Recreation Area is approached from U. S. Hwy. 80, the clinal trend is again repeated, although less dramatically. In the area 8.1 miles north of Hwy. 80 on the road to the Picacho area, var. *phenicodonta* occurs in a frequency of less than 1.0 percent. At 11.7 miles north of the above locality the frequency climbs to 9.0 percent, and at the edge of the Colorado River the frequency reaches 15.0 percent.

Approximately 30 miles to the southwest of Yuma, near the confluence of the Rio Hardy and the Colorado River, in Mexico, a population sample of over 100 individuals includes only *phenicodonta* plants. Thirty-five miles to the south, near the mouth of the Rio Hardy, two closely adjacent samples, comprising 465 plants, average 90 percent *phenicodonta* individuals. Approximately 75 miles east of these three localities, along Mexico Hwy. 2, the frequency of *phenicodonta* drops to 4.7 percent and continues to decline still farther east from this point. Although the *E. farinosa* population samples in Mexico are few, they agree with the basic distribution pattern near Blythe. A sampling of *E. farinosa* along the Colorado River to the immediate north of Blythe, further confirms this clinal distribution pattern. In this area U. S. Hwy. 95 closely follows the course of the Colorado River for approximately 27 miles. An overall frequency of 84.8 percent *phenicodonta* individuals

occurs in the 27 mile interval. North of this area Hwy. 95 takes a north-westward course away from the Colorado River and it is at this point that the frequency of *phenicodonta* plants begins to decline and continues to decrease rapidly as one travels farther away from the Colorado River. If on the other hand, populations are sampled in an eastward direction, it is found that the frequency of *phenicodonta* plants increases as the Colorado River is approached and that they reach their highest incidence of 67.0 percent adjacent to the river in the Earp, California-Parker, Arizona area and to the north. Still farther north, with sampling along the road leading to the Chemehuevi Valley Indian Reservation, the pattern is repeated again. As the Colorado River is approached the proportion of *phenicodonta* in the populations progressively increases from zero (about 15 miles west of the river) to about 20 percent (within one or two hundred yards of the river). Twenty miles to the north in the Topock, Arizona area, a low incidence of 2.0 percent *phenicodonta* plants found at the river's edge quickly drops to zero within less than 0.2 miles from the river. Another 35 miles to the north, where Nevada State Highway 77 crosses the Colorado River, the pattern repeats, with *E. farinosa* populations within a quarter mile of the river containing approximately 20.0 percent *phenicodonta* individuals and with the frequency of these plants decreasing rapidly to zero at less than a mile from the river either in an eastward or westward direction.

In Arizona, other than along or relatively near the Colorado River valley, this writer has so far found only a single area where var. *phenicodonta* occurs in appreciable numbers. This locality is in south-central Arizona, in the Granite Reef Dam vicinity, about 10 miles northeast of Mesa, Arizona.

This site is most remarkable, since in a very small area it duplicates the pattern of distribution observed for the two varieties of *E. farinosa* in and around the much more extensive area of the Colorado River valley. Approaching this Granite Reef Dam locality from the south, one observes that within the interval of 2.2-0.4 miles from the margin of the canyon, the frequency of *phenicodonta* plants averages between 1.0 to 2.0 percent of the populations. In the interval between 0.4 miles south of the canyon and the canyon's south edge there is a progressive increase in *phenicodonta* individuals to 11.0 percent and in the next 0.2 mile interval, as one begins to descend into the canyon toward the Salt River, the frequency sharply increases to 37.0 percent and then to 62.0 percent within the next 0.3 miles. An even higher incidence of 88.4 percent *phenicodonta* plants is encountered at the base of the north wall of the canyon, essentially on the upper banks of the river.

While the association of var. *phenicodonta* with water courses is a prominent feature of its regional, as well as its local distribution pattern, it is apparent that relatively local concentrations of the variety are also found in another kind of habitat. The most notable of these occurs at the west base of the Granite Mountains, 0.2 miles south of the inter-

section of the road to Twentynine Palms with the road to Desert Center, California. This area is conspicuous because of the large sand dune that sprawls on the west slope of the Granite Mountains. Within and adjacent to a sandy wash that spills westward from these mountains, *E. farinosa phenicodonta* attains a frequency of 70.0 percent. Sampling to the immediate south of this locality reveals that this frequency rapidly drops to near zero within less than 5.0 miles, but again increases to about 17.0 percent in the populations at the southeast base of the Coxcomb Mountains. Continuing still farther south toward Desert Center this variety decreases to one percent or less of the populations. Approximately 15 miles north of the Granite Mountains locality, a concentration of *phenicodonta* attaining a frequency of about 20.0 percent occurs in the Iron Mountains. Another 33 miles to the north, approximately a 20.0 percent concentration of *phenicodonta* is found on the lower south-east-facing slope of Clipper Mountain, immediately northwest of Danby, California. In Arizona along U. S. Hwy. 80 at the summit of Mohawk Pass, immediately east of the town of Mohawk, var. *phenicodonta* locally makes up 54.0 percent of the population. Proceeding either east or west from this pass in the Mohawk Mountains, one descends and a rapid decrease in the frequency of *phenicodonta* plants occurs.

In Sonora, Mexico, where very little information on populations of *E. farinosa* is available, an examination of herbarium specimens suggests a most interesting geographic distribution of the two flower color forms of *E. farinosa*. Variety *phenicodonta* generally seems to occur abundantly only near the coast as far south as the latitude of Tiburon Island, and the yellow flowered populations appear to occupy largely the inland areas. Population samples are badly needed from this area of Mexico to establish if this suggested distribution pattern is correct.

Thus the data available from populations of *E. farinosa* indicate that *phenicodonta* is generally associated with major water courses or is largely confined to higher elevations of the California and Arizona deserts, and may be generally limited to the coastal area of the Sonoran Desert of Mexico.

INHERITANCE OF FLOWER COLOR

While a great deal yet remains to be learned about the inheritance of flower color in *E. farinosa*, some interesting observations from experimental crosses as well as natural populations shed some light on this important aspect. One of the first facts established was that when progeny are grown from *E. farinosa farinosa* and *phenicodonta*, where these taxa grow sympatrically in about equal proportions, both varieties can be obtained in the next generation from some of the plants belonging either to var. *farinosa* or *phenicodonta*. This progeny test clearly demonstrates that where the two varieties are sympatric they interbreed. This observation also suggests a simple inheritance for flower color. However,

an examination of natural populations reveals that there is the following additional complication. For while disk floret coloration as discussed above appears to be inherited in a relatively simple, perhaps single gene fashion, a survey of over 4000 individuals in natural populations shows a low incidence of individuals possessing brownish-purple anthers with corollas that are yellow or only slightly tinged with reddish-purple. However, this same sampling of plants has failed to reveal the reciprocal combination of yellow anthers and brownish-purple corollas in the disk florets. This observation seems to indicate that anther and corolla color are not determined by two independently segregating genetic factors, one for anther color and another for corolla color. Instead, it appears likely that one genetic factor produces yellow anthers and corollas, a second genetic factor produces brown anthers, with little or no effect on corolla color, and that a third factor produces brownish-purple anthers and corollas in the disk florets. This genetic scheme would explain the absence of plants with brownish-purple disk corollas and yellow anthers.

A similar inheritance pattern is seen in natural intergeneric hybrids between *E. farinosa* and *Geraea canescens*. Eleven such hybrids have been reported to date and of these, two had entirely brownish-purple disks. A third hybrid had yellow disk corollas and brownish-purple anthers, whereas the remaining eight hybrids had entirely yellow floral parts (Kyhos, 1967). *Geraea canescens* invariably has corollas and anthers that range in color from yellow to yellowish-orange, therefore the brownish-purple disk coloration in the intergeneric hybrid had to be inherited from *E. farinosa* in a dominant fashion. These observations reveal that the brownish-purple pigmentation of the disk corollas and anthers is transmitted to the hybrid in the same manner as in progeny of *E. farinosa*. It has not yet been possible by controlled crosses, however, to produce a large enough progeny in *E. farinosa* to fully examine the mode of inheritance of the three flower color forms. This is largely due to the difficulty of germinating the fruits of *E. farinosa* and the reluctance of this species to flower under greenhouse conditions.

Interspecific hybrids experimentally produced between *E. farinosa phenicodonta* and the yellow disk flowered *E. frutescens* further support an interpretation that flower color is probably inherited in a relatively simple way. These F₁ hybrids have all segregated into two classes: either they have had entirely yellow disk corollas and anthers, or these structures have been brownish-purple. Moreover, they have segregated in essentially equal frequencies with a Chi-square value conforming well to the 1:1 ratio expected in the test cross of a heterozygous dominant parent to a homozygous recessive one (see table 1).

Finally, controlled intraspecific crosses between individuals of *E. farinosa farinosa* and *phenicodonta* also indicate a relatively simple genetic basis for disk coloration, depending on which individuals are used as parents. So far in these crosses one of two things occurs. Either all the progeny are var. *phenicodonta* or the progeny segregate for the

TABLE 1. SEGREGATION OF DISK COLORATION IN F₁ HYBRIDS BETWEEN ENCELIA FRUTESCENS AND ENCELIA FARINOSA PHENICODONTA

	<i>observed</i>	<i>expected</i>	<i>d</i>	<i>d</i> ²		
Yellow disks	21	21	0	0	$X^2 = 0.0$	$p = .99$
Brownish-purple disks	21	21	0	0		

two varieties in a frequency that conforms well to a 1:1 ratio with the Chi-square test (table 2).

OBSERVATIONS ON POLLINATORS

Since disk floret color differentiates *E. farinosa farinosa* from *phenicodonta*, it was important to observe if natural pollinators distinguish between these two color forms and in so doing were perhaps responsible for the remarkable geographic distribution of these plant taxa. In line with this approach twelve populations were studied within and adjacent to the Colorado River valley, between Blythe and Needles, California. Six populations were in the area of sympatry of *farinosa* and *phenicodonta* and the remaining six were in areas occupied only by *farinosa*, between 10 to 14 miles removed from the Colorado River. In all twelve populations it was found that pollen shed in both *farinosa* and *phenicodonta* begins about 9:00 a.m. and ceases in the early afternoon, with some day to day variation apparently depending on the weather. Pollen was shed somewhat earlier on warm sunny days than on cool cloudy days. Nevertheless, on any given day the two forms of *E. farinosa* always shed essentially synchronously, indicating that temporal factors apparently provide no reproductive isolation.

The remaining important aspect was whether different pollinators were attracted to the two flower color types. An examination of the six sympatric populations of *farinosa* and *phenicodonta* demonstrated a variety of flower visiting insects, including diptera, hymenoptera, lepidoptera, homoptera, and coleoptera. All of the species in each of these insect orders occurred on both varieties of *E. farinosa*. Moreover, they fly from individuals of each *E. farinosa* variety in a random fashion, with individual insects showing no preference for one flower color. The most important pollinator in each of these populations proved to be a small beetle, *Tanaops abdominalis* Le Conte, of the Malachiidae, which occurred in a frequency over 10 times greater than all of the other insect species combined. This beetle species moved from flower head to flower head, efficiently pushing among the disk florets, inadvertently picking up pollen along the way and then flying quickly and quite accurately to the next flowering head of *E. farinosa*, which might be either that of *farinosa* or *phenicodonta*.

TABLE 2. SEGREGATION OF DISK COLORATION IN PROGENY OF ENCELIA FARINOSA FARINOSA \times ENCELIA FARINOSA PHENICODONTA

	<i>observed</i>	<i>expected</i>	<i>d</i>	<i>d</i> ²
Yellow disks	19	18	1	1
				$X^2 = .111$
				$p = >.70$
Brownish-purple disks	17	18	1	1

DISCUSSION

Encelia farinosa phenicodonta has been recognized as a form or variety of *Encelia farinosa* Gray, for approximately fifty years (Blake, 1913; Johnston, 1924). Botanists who have dealt with these taxa apparently considered them to be simply flower color variants that differ only in this seemingly trivial aspect (Abrams and Ferris, 1960; Blake, 1913; Johnston, 1924; Munz, 1959; Shreve and Wiggins, 1964). However, closer scrutiny provides compelling evidence that these taxa have a much deeper and most intriguing biological significance. The distribution pattern of these taxa is quite remarkable and seemingly can only be interpreted as resulting from natural selection. It surely cannot be fortuitous that comparatively high frequencies of *phenicodonta* plants occur as a narrow, occasionally interrupted strand closely following the course of the Colorado River for approximately 260 miles north of the main body of this taxon (fig. 1). It seems even less likely that chance is a significant determinant in this remarkable distribution, when one notes that this 260 mile strand of *phenicodonta* is completely included within the range of *Encelia farinosa farinosa* and that these two taxa are sympatric along this entire 260 mile interval, and are known to interbreed with no evidence of reproductive isolation. In seeking an understanding of what selective forces may be operating to produce this striking distribution pattern, we perhaps can gain insight from the observation that the pattern along the Colorado River valley is dramatically repeated on a much smaller scale at Granite Reef Dam in east-central Arizona, near the city of Mesa. Both in the Colorado River valley and the Granite Reef Dam area of Arizona the populations of *Encelia farinosa* with the greatest proportion of *phenicodonta* plants occur closest to the water in these drainage systems, and as one travels away from the water course the frequency of *phenicodonta* individuals progressively declines until individuals of var. *farinosa* entirely replace *phenicodonta*. These observations suggest that in some manner water is important in determining the distribution of *E. farinosa farinosa* and *phenicodonta*. The apparent predominance of *phenicodonta* populations near the coast, with *farinosa* populations characterizing the more inland areas of Sonora, Mexico, again lends support to the idea that effective moisture is a crucial factor in the distribution of these two taxa. The credibility of this interpretation is further enhanced when it is recalled that the comparatively small

local concentrations of *phenicodonta* individuals, which occur away from water courses and large bodies of water, are found at higher elevations in the deserts of California and Arizona (e.g., at Mohawk Pass, Arizona, near Hwy. 80; and at Lobecks Pass near Hwy. 95, about 15 miles south of Needles, California; and in the Iron, Granite, Coxcomb Mts., and on Clipper Mt., all located in the Mohave Desert of California and its transition to the Colorado Desert to the south). These desert mountain ranges characteristically receive greater amounts of rainfall than the surrounding lower desert and thus in this regard would be similar to the habitats near water courses and large bodies of water.

It might be argued that the water course habitats, higher desert elevations, and coastal areas would provide cooler temperatures and thus temperature itself may be a critical factor in the distribution of these taxa. It is obvious that lower temperatures would tend to reduce transpiration and hence increase the amount of effective moisture. Thus it is important to separate the action of these two factors. An examination of maximum, minimum, and mean temperatures in the journal, *Climatologic Data*, through the ranges of these two taxa reveals no correlation with their distribution. If water stress is physiologically crucial in determining where these two taxa grow, it remains obscure how this factor is invariably associated with a seemingly unrelated characteristic such as disk flower coloration, except perhaps through pleiotropy or an extremely close genetic linkage.

On the other hand, the possibility cannot as yet be totally ruled out that flower color is itself adaptive. For example, it might be imagined that a pollinator preferring brownish-purple disks in *Encelia* is limited to areas of greater moisture in the desert, however no such evidence has yet been obtained. In fact, field observations support quite the opposite conclusion, namely, that the effective pollinators do not discriminate between *farinosa* and *phenicodonta* and progeny tests of these two taxa where they are sympatric bear this out.

While the selective factors which produce the remarkable distribution pattern of *farinosa* and *phenicodonta* are as yet unknown, some insight into the possible origin of these very similar taxa can be gained from what is known about the genetic basis of their differences. The available evidence indicates that these taxa are based on comparatively simple genetic differences. Brownish-purple disk floret coloration apparently can be inherited in a dominant, single gene fashion. Individuals of *phenicodonta* when crossed to var. *farinosa* either have produced progeny all with brownish-purple disks or in other crosses the progeny have segregated for brownish-purple and yellow disks in essentially equal frequencies. This rather simple situation becomes slightly more complicated, since many natural populations include a low frequency of individuals possessing yellow disk corollas associated with brownish-purple anthers. However, even with this additional aspect the genetic difference between these taxa appears to be quite simple, with disk

TABLE 3. LOCALITIES OF POPULATION SAMPLES

After each locality the letter t followed by a number indicates how many *Encelia farinosa farinosa* individuals occurred in the sample, whereas a number preceded by the letter p indicates how many *E. farinosa phenicodonta* individuals were in the sample.

ARIZONA. Near hwy 60-70, 2 mi E Colorado R., t-0, p-45; 1 mi farther E, t-10, p-240; 1 mi farther E, t-2, p-77; 1 mi farther E, t-17, p-122; 1 mi farther E, t-34, p-76; 1 mi farther E, t-33, p-251; 1 mi farther E, t-6, p-17; 1 mi farther E, t-30, p-14; 1 mi farther E, t-50, p-28; 1 mi farther E, t-28, p-3; 1 mi farther E, t-130, p-32; 1 mi farther E, t-157, p-16; 1 mi farther E, t-55, p-4, near hwy 80, 13.4 mi E jct with San Luis rd, t-96, p-4; 2 mi farther E, t-99, p-1, 1.7 mi farther E, t-337, p-6; 2.5 mi farther E, t-87, p-22, near hwy 80, 0.3 mi W Mohawk Pass summit, t-46, p-54; 1.1 mi E Mohawk Pass summit, t-170, p-30; hwy 80, 14 mi W jct with Theba rd, t-195, p-5; hwy 80, 15.9 mi W Buckeye, t-200, p-0; near hwy 80, 2.8 mi E jct with hwy 72, t-99, p-1; near hwy 80, 21 mi W jct with hwy 72, t-200, p-0; 9.3 mi N Wenden, t-200, p-0, rd to Dome, 6.3 mi N of hwy 80, t-94, p-11; 5.3 mi N of Tucson, t-200, p-0; 3-4 mi S Parker Dam, t-69, p-131; edge S rim Salt R. canyon at Granite Reef Dam, t-89; p-11; 0.8 mi farther S, t-98, p-2; 1.5-2 mi farther S, t-99, p-1; 2.2-2.7 mi farther S, t-152; p-3; 0.2 mi N, S rim Salt R. canyon, t-63, p-37; 0.3 mi farther N, t-38, p-62; N bank Salt R. at Granite Reef Dam, t-35, p-265.

CALIFORNIA. Hwy 60-70, 11.2 mi W Colorado R, t-110, p-24; near hwy 95, 8.4-33.4 mi N jct with hwy 60-70, t-106, p-384; at 34.6 mi N, above jct, t-48, p-532, and one plant with a light purple disk; at 46.5 mi N, above jct, t-48, p-4; Vidal Jct., t-39, p-1, 1 mi E Vidal Jct., t-16, p-7; 1 mi farther E, t-16, p-4; 0.8 mi farther E, t-172, p-28; from Earp to 7.4 mi N, t-17, p-35; Parker to 5 mi S, t-45, p-135; Vidal Jct. to 4 mi N, t-92, p-8; 1.5 mi farther N, t-99, p-1, 1.7 mi farther N, t-200, p-0; 1.2 mi farther N, t-290, p-10, 1 mi farther N, t-200, p-0, jct hwy 95 with rd to Chemehuevi Valley Indian Res., t-200, p-0; 4.8 mi farther E, t-100, p-0; 5.2 mi farther E, t-94, p-6; 4 mi farther E, t-49, p-1, 3.4 mi farther E, t-16, p-1, bank Colorado R. at Chemehuevi Indian Res., t-79, p-21; 4.3-5.5 mi W Colorado R. near hwy 66, t-100, p-0, W bank Colorado R. near hwy 66, t-98, p-2, 1.1 mi N Needles, t-99, p-1, S slope Clipper Mt. near Danby, t-182, p-38; hwy 95 at Lobecks Pass near jct with hwy 66, t-95, p-5, near rd from Blythe to Rice, 2 mi N Riverside Co. dump, t-30, p-70; 4.1 mi N, above, t-62, p-38, 3.5 mi farther N, t-190, p-10, 5.9 mi farther N, t-200, p-0; summit at S end Iron Mts., t-64, p-4; 0.4 mi farther W, t-26, p-0; 0.1 mi farther W, t-284, p-16; 0.5 mi N near summit Iron Mts., t-171, p-29; 0.5 mi S jct of rd to Desert Center and Twentynine Palms rd., t-44, p-173, 5.6 mi S of above, t-99, p-1; 8.3 mi farther S, t-83, p-17; 1 mi W of Desert Center, t-99, p-1; 0.1 mi N hwy 60-70, near rd to Twentynine Palms through Joshua Tree Nat. Mon., t-300, p-0; Morongo Wash, 2.6 mi N hwy 60-70, t-300, p-0; White Water Canyon, NW Palm Springs, t-400, p-2; 1 mi S, S border Anza-Borrego State Park near rd S2, t-200, p-0; Panamint Valley, 0.5 mi W Darwin Springs, t-200, p-0; 8.1 mi N hwy 80 near rd to Picacho Resort Area, t-107, p-1; 11.7 mi N, above, t-91, p-9; S bank Colorado R. at Picacho Resort Area, t-85, p-15.

MEXICO. 4-5 km S San Felipe, Baja California, t-0, p-100; 180 km N San Felipe, Baja California, t-0, p-100; 122 km N San Felipe, Baja California, t-19, p-142; 115 km N San Felipe, Baja California, t-24, p-280; Mexican hwy 2, 50 mi E San Luis, Sonora, t-100, p-5; Mexican hwy 2, 106 mi E San Luis, Sonora, t-96, p-4; Mexican hwy 2, 16 mi S Sonoyta, Sonora, t-98, p-2; 12.7 mi W Caborca, Sonora, t-22, p-123.

NEVADA. Near hwy 77, 0.3 mi W of Colorado R., t-90, p-23; 5.9 mi W, above, t-153, p-1.

corolla and anther coloration in the great majority of individuals matching one another. Despite the relatively simple genetic basis for disk floret coloration, this minor phenetic difference appears to be biologically very important, perhaps in itself or possibly it is inextricably associated with some factor that is crucial in determining where these taxa can survive. In this situation the sympatric origin of one taxon from the other appears quite feasible, with this simple genetic difference providing the means by which a new or different habitat could be occupied, resulting secondarily in allopatry of the two taxa in much of their ranges, rather than allopatry being a necessary prerequisite for the differentiation of these taxa.

The present distribution of *E. farinosa farinosa* and *phenicodonta* suggests that the latter was previously more widespread, perhaps within fairly recent times. *Phenicodonta* in the northern portions of the Sonoran Desert not only occurs in high frequency, as a more or less continuous strand, along the Colorado River valley, but it is found also as isolated populations, some of which are quite small and far removed from the great concentrations of *phenicodonta*. These scattered, well isolated populations of *phenicodonta* may represent remnants of a once more extensive distribution. The converse situation of scattered, well isolated populations of *farinosa* in areas populated predominantly by *phenicodonta* is unknown. This suggests that perhaps during a period such as the hypsithermal, when comparatively warm, moist climates may have extended farther north than today (Martin, 1963), *phenicodonta* may also have occurred farther north than at present. With the decline of the hypsithermal, *phenicodonta* may have retreated to the south, leaving small isolated populations surviving in favorable local sites as evidence of this former distribution, while *farinosa* came to occupy most of the remainder of the Sonoran Desert, now untenable for *phenicodonta*.

The relationships of *Encelia farinosa farinosa* and *phenicodonta* somewhat parallel those described for *Linanthus parryae* by Epling, Lewis, and Ball (1960). In both *Linanthus* and *Encelia* different flower colors, which have a relatively simple inheritance, seem to be indicative of more deep-seated biological differences between individuals which apparently interbreed freely. In each of these cases, the importance of these distinct flower color differences as indicators of a crucial biological difference is revealed by the local and regional distribution patterns of these flower color types. The distribution patterns in *Linanthus* and *Encelia* appear to be the result of natural selection, but in neither case is the nature of the selective forces known. However, the relatively simple genetic differences of the individuals possessing these distinct adaptations offer hope that their adaptations are commensurately simple and hence ultimately can be understood.

ACKNOWLEDGMENTS

The writer is indebted to H. B. Leech of the California Academy of Sciences, who kindly identified the beetle, *Tanaops abdominalis* Le Conte, which pollinates *Encelia farinosa*. I am also grateful to Albert Johnson, Spencer Smith-White, and Keith Jones who generously provided data on several population samples in Mexico. Finally, the support for a portion of this work by National Science Foundation grant GB 6098 is gratefully acknowledged.

SUMMARY

An unusual geographic distribution of *Encelia farinosa farinosa* and *E. farinosa phenicodonta* is presented as evidence that these taxa have a much greater biological significance than mere flower color variants. Crossing experiments indicate that the flower color differences of these taxa can be inherited in a single gene, dominant fashion. The association between flower color differences and the survival of these taxa in particular geographic areas remains unresolved.

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